

THE SETACEOUS SPECIES OF *BATRACHOSPERMUM*
(RHODOPHYTA): A RE-EVALUATION OF *B. atrum* (Hudson) Harvey
AND *B. puiggarianum* Grunow INCLUDING THE DESCRIPTION OF
B. diatyches SP. NOV. FROM TASMANIA, AUSTRALIA.

by

T.J. ENTWISLE*

ABSTRACT

Entwisle, T.J. The setaceous species of *Batrachospermum* (Rhodophyta): a re-evaluation of *B. atrum* (Hudson) Harvey and *B. puiggarianum* Grunow including the description of *B. diatyches* sp. nov. from Tasmania, Australia. *Muelleria* 7(4): 425–445 (1992). — Species concepts among the setaceous *Batrachospermum* (those species with compact gonimoblasts which are exerted beyond reduced whorls of fascicles) are clarified. *Batrachospermum atrum* (Hudson) Harvey is a widespread and variable species throughout the world, ranging between two extreme growth forms: one with mostly cylindrical cells in little-branched fascicles forming relatively open whorls, the other with more rounded or barrel-shaped cells in richly-branched fascicles forming compact whorls. Mature plants of *B. puiggarianum* Grunow, from southern-central Africa and South America, are similar to those of *B. atrum* with compact whorls, but young thalli of *B. puiggarianum* are quite distinct, bearing reduced fascicles which form a tight cortical layer around the axial filament (individual fascicle structure not being discernible). *Batrachospermum diatyches* Entwisle sp. nov., a littoral alga found only in a few mountain lakes in Tasmania, Australia, differs substantially from the other two setaceous *Batrachospermum* species. The thallus apex is blunt rather than acute with the large apical cell ($> 10\ \mu\text{m}$ diameter) overtopped by the first whorls of primary laterals; the axial cells are 2.5 times the diameter of the broad ($> 9\ \mu\text{m}$ diameter) rhizoidal filaments; and the fascicles consist of tapered, scarcely branched filaments without constrictions at the crosswalls. Historical remarks on *B. atrum*, *B. gallaei* var. *longipilum* Skuja nom. nud. and *B. nothogae* Skuja nom. nud. are provided, incorporating some previously unpublished illustrations, correspondence and notes of Heinrichs Skuja. The reputedly setaceous species, *B. africanum* Rabenhorst, *B. orthostichum* Skuja, *B. patens* Suhr and *B. tenuissimum* Bory are re-evaluated.

INTRODUCTION

The setaceous species of *Batrachospermum* have compact, globular or semi-globular gonimoblasts which protrude beyond the reduced (short and little-branched) whorls of lateral fascicles. The carpogonial branches are relatively straight and bear symmetrical carpogonia like those found in species with more robust whorl fascicles such as *B. virgatum* (Kützinger) Sirodot. For this reason, the setaceous species have been recently included in a broadly circumscribed section *Viridia* Sirodot (Necchi 1990, Necchi & Entwisle 1990).

Earlier authors (e.g. Israelson 1942, Mori 1975) retained the grouping devised by Sirodot (1884), which included all setaceous species in their own section, *Setacea* Sirodot. The discovery of taxa with whorl development intermediate between typical *Setacea* and the 'well-developed whorl' morphology more commonly found in *Batrachospermum*, and of 'reduced whorl' plants with contorted or twisted carpogonial branches (usually referred to the section *Contorta* Skuja), has made the circumscription of the section *Setacea* inconsistent and impractical (Necchi & Entwisle 1990). Nevertheless, the algae traditionally relegated to the

* National Herbarium of Victoria, Birdwood Ave, South Yarra, Victoria, Australia 3141.

section *Setacea* are centred around an entity generally called *B. atrum* (= *B. dilenii*). The full morphological range expressed by members of this species complex had to be established before any putative taxa displaying reduced whorl morphology could be either synonymized with *B. atrum* or established as independent entities. Algae collected sporadically over the last 75 years from New South Wales and Tasmania included material of at least one distinctive setaceous *Batrachospermum*.

This re-evaluation of the setaceous *Batrachospermum* species is based on extensive fresh collections from south-eastern Australia, herbarium material from Australia, New Zealand, Europe and South and North America, unpublished notes, letters and illustrations by Heinrich Skuja, and relevant protologues and other published literature.

MATERIALS AND METHODS

Wet material was preserved initially in 5% commercial formalin which was later replaced with FAA (see Entwisle 1989) or 70% alcohol with 5% glycerol. Dry material prepared for microscopic observations was rehydrated with 20% detergent solution and gently heated. All microscope preparations were stained with 1% aniline blue (with 4% molar HCl) and mounted in 'Karo'. Herbarium abbreviations follow Holmgren *et al.* 1981.

KEY TO SPECIES

1. Thallus apex blunt, apical cell overtopped by primary laterals; axial cells < 2.5 times the diameter of the rhizoidal filaments..... 1. *B. diatyches*
1. Thallus apex acute, apical cell protruding from beyond primary laterals; axial cells > 2.5 times the diameter of the rhizoidal filaments..... 2
2. Fascicle structure discernible at least in young whorls; 2-celled primary laterals occurring within the first 10 axial cells from apex..... 2. *B. atrum*
2. Fascicle structure always indiscernible (young thalli tightly corticated, almost as found in the Lemnaceae); 2-celled primary laterals usually not occurring within 10 axial cells of the apex 3. *B. puiggarianum*

SPECIES ACCOUNTS

1. ***Batrachospermum diatyches*** Entwisle *sp. nov.*
Batrachospermum nothogae Skuja *nom. nud., pro parte.*

Batrachospermum atrum affinis apicibus thallorum obtusis cellula inclose amen (majored 10 µm diametro), cellulis apicibus filamentous rhizoideorum minoribus 2.5 plo diametro, filamentis rhizoideorum latis (majoribus 9 µm diametro), et filamentis fasciculorum gradatim decrescentibus, septis non constrictis differt.

HOLOTYPE: Lake Meston, north-central Tasmania. Epilithic in littoral zone of northern portion of lake. Water acidic (pH 5.7). Coll. *P.A. Tyler s.n.* 10.iii.1988, MEL 1587821. **ISOTYPE:** MEL 1587822, BM, SP, UPC.

Thalli entangled, individual plants firm, wiry, up to 6 cm long, 70–110 µm diameter (60–100 µm at internodes), dark-brown; branching irregular, sparse, acute to perpendicular. *Whorls* inconspicuous, reduced to ring of procumbent fascicles directed towards apex, separated; internodes 50–200 µm long. *Thallus apices* blunt, densely sheathed in fascicles; apical cell hemispherical, 7–13 µm long, 12–14 µm diameter; subsequent axial cells firstly discoid, then short-barrel shaped, and finally cylindrical; first laterals cut c. 2 axial cells back from apex, becoming 2-celled almost immediately; young fascicles open, intercalary cells cylindrical, 8–12 µm long, 6–10 µm diameter, L/D 1–1.5. *Young central axis* (100–500 µm from apical cell) consisting of axial cells 13–27 µm diameter,

clothed by rhizoidal filaments 10–15 μm diameter, axial cell 1.4–1.8 times broader than rhizoidal filaments. *Mature central axis* consisting of narrow axial cells, 22–28 μm diameter, clothed by regular layers (resulting in brick-like pattern of cells) of rhizoidal filaments, 10–16 μm diameter, axial cells < 2.5 times as broad as rhizoidal filaments. *Fascicles* 2 per pericentral cell (plus rhizoidal filament), finger-like, projected towards apex, unbranched (single lateral cells cut off distal cell are presumably spermatangial mother cells), tapering, not constricted at cross walls, cell storeys 4–6, branching 0–2 times; proximal cells initially cylindrical, becoming ovoid, 15–20 μm long, 8–10 μm diameter; intercalary cells more or less cylindrical, 8–12 μm long, 6–10 μm diameter; apical cell irregularly conical, apex rounded or pointed, 8–13 μm long, *c.* 10 μm diameter, terminated by hair, up to 90 μm long, which is apparently regularly shed and replaced (concentric empty cell-walls are often all that remains of the terminal hair). *Secondary fascicles* rare, usually single celled (multicellular secondary fascicles occurring sporadically in older thalli).

Plants monoecious. *Carpogonial branches* rare, borne on proximal cell of primary fascicle, protruding from whorl, 2–3 cells long, curved or straight, with compact, few-celled involucre bracts not overlapping trichogyne. *Carpogonia* 44–46 μm long; trichogyne elongate to swollen, fusiform to obovate, 32–38 μm long, 5–10 μm diameter. *Spermatangia* cut off obliquely from distal cell of primary fascicles, ellipsoid to obovoid, 8–10 μm long, 6–8 μm diameter. *Gonimoblast* usually 1 per whorl, sparse, more or less globular, protruding wart-like from primary fascicle whorl, centre displaced to one side of thallus, 80–220 μm in diameter; carposporangia obovoid to globular, 15–19 μm long, 6–18 μm diameter.

Audouinelloid filaments twining around older thalli presumably resulting from germinated carpospores (epiphytic 'Chantransia' stage) or else playing some attachment role. (Figs 1, 2a-b)

DIAGNOSTIC FEATURES:

Batrachospermum diatyches is similar to *B. atrum* in habit and morphology but has blunt thallus apices with an embedded, large (> 10 μm diameter) apical cell; axial cells < 2.5 times the diameter of the broad (> 9 μm diameter) rhizoidal filaments; and fascicle filaments gradually tapering and not constricted at crosswalls.

DISTRIBUTION & HABITAT:

Western Tasmania in relatively high altitude (> 300 m above sea level), acidic (pH < 6) lakes. All collections made during summer and early-autumn.

OTHER SPECIMENS EXAMINED:

Tasmania — Lake Pedder, south-west Tasmania, 2.iii.1966, P.A. Tyler 660302/2 (MEL); Dove Lake, Cradle Mountain area, - .ii.1928, F. Perin s.n. (NSW), 13.xii.1973, A.B. Cribb 773.3 p.p. (BRI).

ETYMOLOGY:

The epithet '*diatyches*' [(Gk) *di* = twice, *atyches* = unfortunate] alludes to two unfortunate events which occurred in 1972 and were associated with the discovery of this taxon:

- 1) the permanent flooding of Lake Pedder to provide a hydroelectricity facility, and
- 2) the death of Heinrichs Skuja (1892–1972) prior to his publishing on this new species.

TAXONOMIC NOTES:

Only a few non-empty spermatangia were observed, so details of these structures are tentative. *Carpogonia* were also scarce, and all *N. diatyches* material

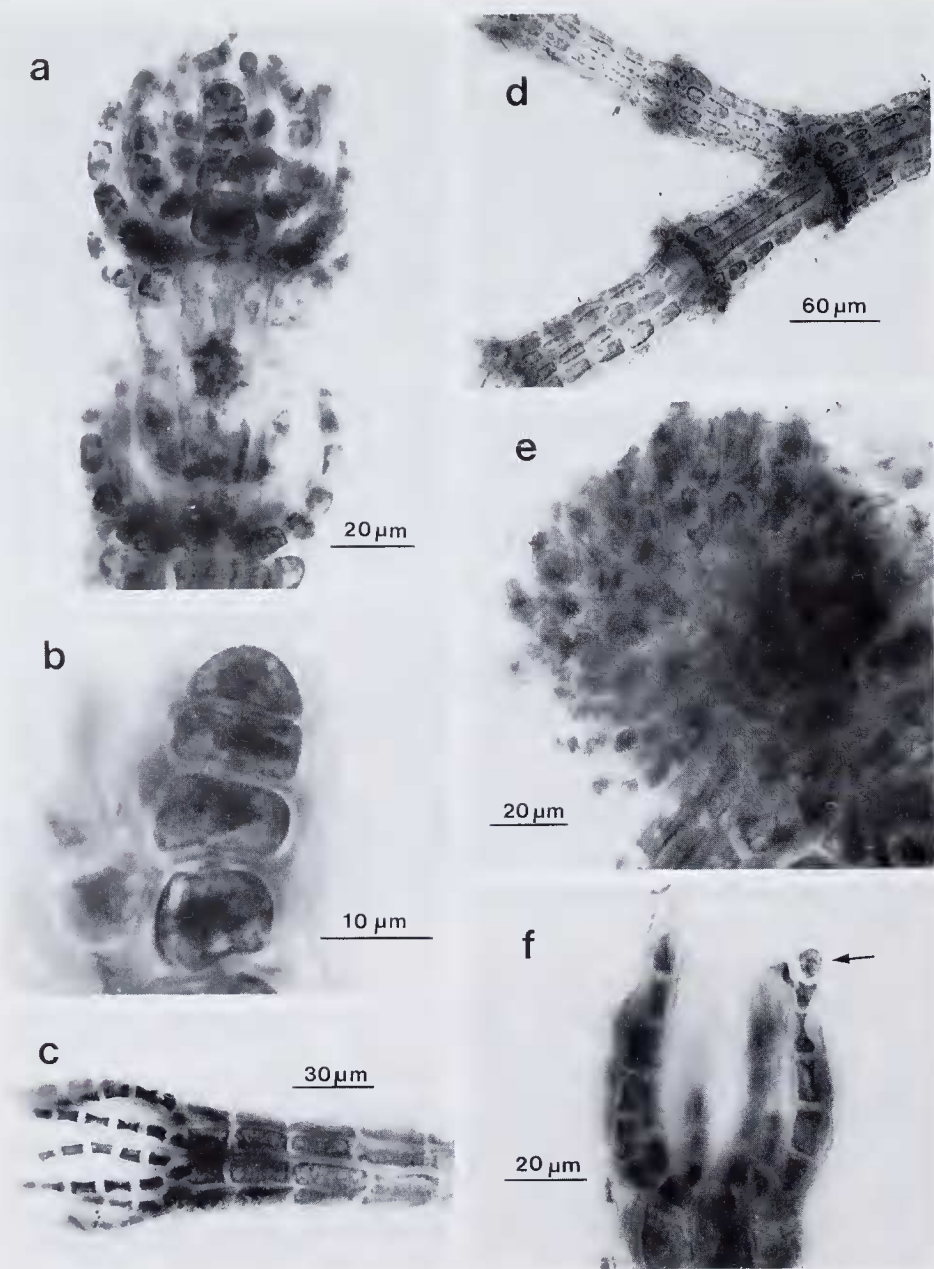


Fig. 1. *Batrachospermum diatyches*. a — thallus apex with apical cell overtopped by young fascicles (Perin s.n.). b — apical cell and first axial cells of thallus (first lateral fascicle directed out of plane of focus on left) (Tyler s.n., iii. 1988). c — whorl of fascicles and rhizoidal filaments in disassociated fragment (Perin s.n.). d — portion of mature thallus with axial cells in focus towards right and rhizoidal filaments towards left (Tyler s.n., iii. 1988). e — gonimoblast attached to thallus at bottom right (Perin s.n.). f — spermatangium (arrow) at tip of lateral fascicle (Perin s.n.).

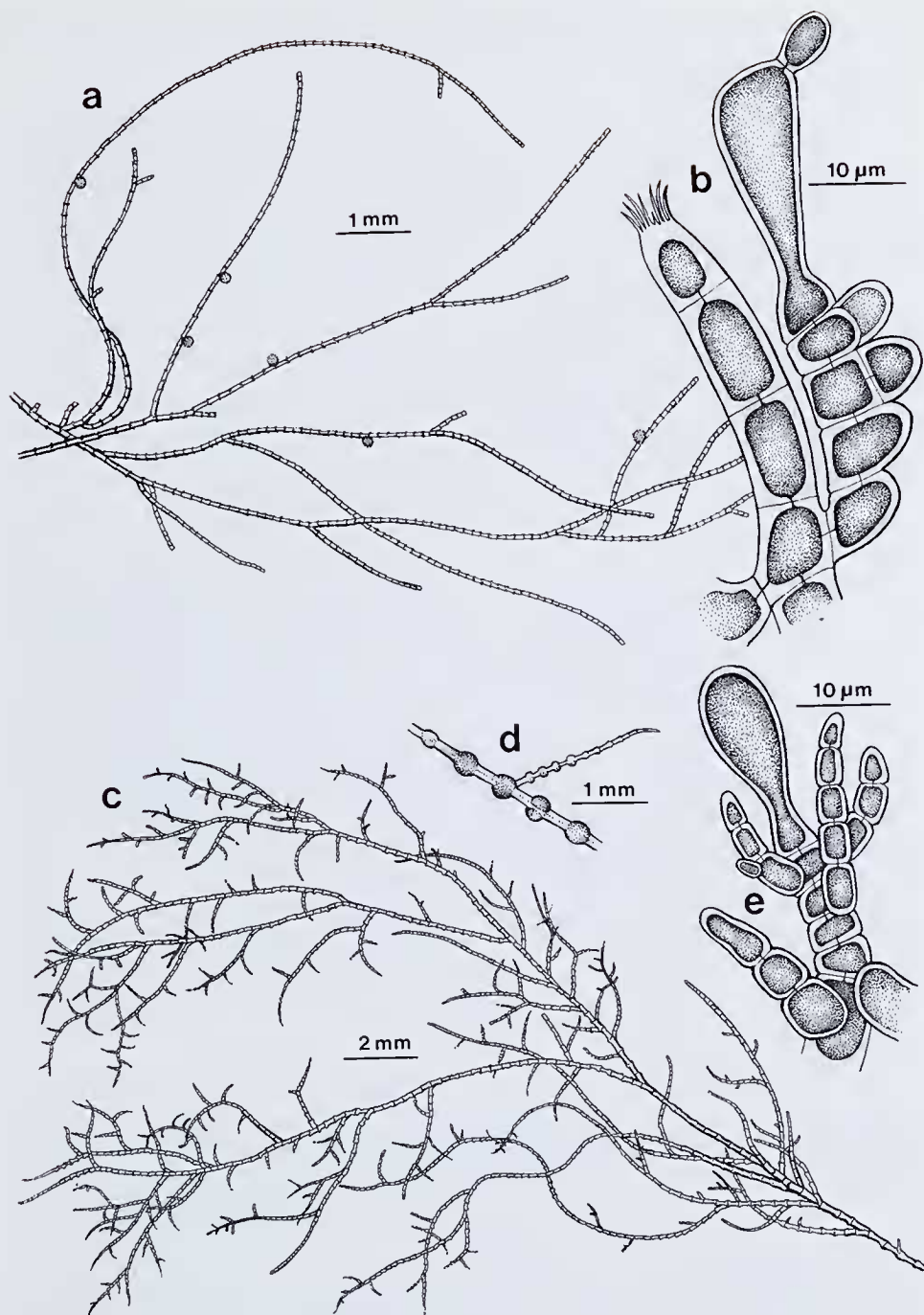


Fig. 2. a,b. *Batrachospermum diatyches* (Tyler s.n., iii.1988). a — habit showing lateral, spherical gonimoblasts. b — carpogonial branch (right), bearing carpogonium with spermatium attached, arising from proximal cell of sterile lateral. Note distal cell wall remains of apparently deciduous hairs on sterile lateral, and 1-celled involucral bracts on cells subtending carpogonium. c-e. *Batrachospermum atrum*. c — habit (Entwistle 1797). d — wart-like gonimoblasts on main branch (Entwistle 1566). e — carpogonial branch with 3-5-celled, occasionally branched involucral bracts (Entwistle 1668).

observed was certainly less 'fertile' than *B. atrum*. Whether this reflects phenological behavior or a peculiarity of the species is not known.

HISTORICAL REMARKS:

In May 1968, Dr Peter Tyler (University of Tasmania) sent Heinrichs Skuja (University of Uppsala, Sweden) a batch of freshwater red algae from Tasmania. Represented in these collections were *B. vagum* (Roth) C. Agardh, *B. gallaei* var. *longipilum* nom. ms. Skuja (first found in New Zealand), and an undescribed setaceous species of *Batrachospermum* to which he had given the manuscript name '*B. nothogae*' (mentioned in Entwistle & Kraft 1984: 217). In a note scribbled on the letter accompanying these specimens, Skuja intimates that the Tasmanian plants might represent a new variety of '*B. nothogae*'.

Skuja explained to Tyler that he already knew of Australian '*B. nothogae*' from dried herbarium material sent to him in 1934. That specimen came from the Blue Mountains in NSW, collected by Dr L.H.S. Lucas in 1918. The only other locality of '*B. nothogae*' known to Skuja was in the Falkland Islands (collected by Lechler in the 1850s from a creek near William Stanleys Haven). This collection was circulated as part of Hohenacker's *Algae Marinae Siccatae* (No. 307) under the name '*B. moniliforme* Roth f. *Conferva atra* Dillwyn' (Skuja-Tyler corr. 13.v.1968)]. Skuja first determined this specimen as *B. dillenii* var. *nothogae* nom. ms. (10.viii.1932), but later decided that the taxon warranted specific rank.

The Tasmanian '*B. nothogae*' was collected in April 1966 from the shores of Lake Pedder, a glacial-formed lake in the mountainous south-west of the state. This pristine lake was characterised (up until 1972) by extensive beaches of quartzite sand washed by acidic, humic waters. Tyler promised to look for more *Batrachospermum nothogae* in the lakes and streams of south-west Tasmania.

In February 1969, Dr Heinrich Skuja excitedly opened a parcel of wet-preserved algae from south-west Tasmania (Skuja-Tyler corr. 19.ii.1969). Disappointingly, although the vial contained good material of what Skuja knew as *B. gallaei* var. *longipilum* nom. ms. (also a setaceous species), there was no '*B. nothogae*' to complete his description of that species (Skuja-Tyler corr. 19.ii.1969). Since none of Tyler's subsequent collections included '*B. nothogae*', he sent the remainder of the 1966 collection to Skuja in March 1972.

In July 1972, Skuja died, apparently without having examined the latest batch of Tasmanian material (which also included two collections of *Batrachospermum* not referable to '*B. nothogae*'). In the same year, Lake Pedder was flooded by the Tasmanian Hydroelectricity Commission in spite of years of intense lobbying by conservationists and environmentalists keen to preserve this lake's unique biology. The surface area of the lake increased by 25 times, and the sandy beach was destroyed.

Just over 10 years later (February 1983), I received a box of vials from Dr R. Moberg, Director of the University of Uppsala Herbarium. Included were 30 specimens from New Zealand and three specimens from Tasmania, all sent to Skuja in early 1972. Although many were dried out, some — including one of the three Tasmanian collections — were in excellent condition. The Tasmanian collections were obviously those sent by Tyler to Skuja in March 1972.

2. *Batrachospermum atrum* (Hudson) Harvey, *Man. brit. Alg.* 120 (1841). *Conferva atra* Hudson, *Fl. angl.* 597 (1798).

HETEROTYPIC SYNONYMS: *B. gallaei* Sirodot, *Batrachospermes* 256, pl. 22 figs 1–7 (1884).

B. dillenii Sirodot, *Batrachospermes* 254, pl. 20 figs 1, 2, pl. 21 figs 1–12, pl. 22 figs 8–13 (1884).

¹ The etymology of the epithet '*nothogae*' is unknown, but the name is presumably derived from the Greek *noth-* = false or spurious, and *-ge* = earth, possibly referring to its brown colour.

B. angolense W. West & G. S. West, *J. Bot.* 35: 2 (1897). *Sirodotia angolensis* (W. West & G. S. West) Skuja, *Bol. Soc. Brot.* 34: 53 (1960).

TYPE: From a little well, in the plain called Gors Bach, between Llanfaethly and Trefadog, Wales. Coll. *S. Brewer s.n.*, prior to 1741 (BM). [Photograph of holotype examined.]

Tufty, stream-inhabiting alga. *Thallus* fine and delicate, to firm and robust, up to 4 cm long and 120–240 μm diameter (90–170 μm at internodes), green to reddish-brown or almost black; branching irregular, sparse to frequent, acute to perpendicular. *Whorls* inconspicuous, ovoid, turnip-shaped to conical, separated except in very old thalli, open and tufty, to compact (like the hair of a clipped poodle), in degenerating plants they may be denuded; internodes 380–800 μm , long. *Thallus apices* tapering, acute; apical cell dome-shaped, 3–8 μm long, 4–8 μm diameter, L/D 0.8–1.5; subsequent axial cells firstly discoid, then globular, and finally long cylindrical; first laterals cut *c.* 3 axial cells back from apex, becoming 2-celled *c.* 8 axial cells from apex; young fascicles compact to open. *Young central axis* [100–500 μm from apical cell] consisting of axial cells 16–32 μm diameter, clothed by rhizoidal filaments 3–8 μm diameter, axial cell 3–8 times broader than rhizoidal filaments. *Mature central axis* consisting of broad axial cells, 25–130 μm diameter, clothed by rows or intertwining bundles of rhizoidal filaments, 3–4 μm diameter. *Fascicles* 2–3 per pericentral cell (plus rhizoidal filament), curved towards apex, branching 0–5 times, with 3–6 cell storeys; proximal cells globular to dome-shaped, 7–12 μm long, 4–8 μm diameter; intercalary cells at first cylindrical to slightly barrel-shaped, or cubic, finally globular to cylindric-ellipsoid, 4–14 μm long, 3–10 μm diameter; apical cell dome-shaped to somewhat ovoid, 4–12 μm long, 4–6 μm diameter; hairs absent, sparse or abundant, 5–160 μm long (but less variable in length within a single population), single-celled. *Secondary fascicles* usually frequent, similar to primary fascicles near axial cell nodes but only unicellular to few-celled away from nodes in younger thalli, eventually extending from one node to next, with or without hairs.

Monoecious or dioecious. *Carpogonial branches* relatively common in primary fascicles, borne on proximal cell of fascicle, protruding from whorl, 3–5 cells long, curved, with compact, few-celled involucre bracts not reaching trichogyne. *Carpogonia* 15–27 μm long; trichogyne inflated, and ovoid, urn-shaped, clavate, fusiform or ellipsoid, 8–16 μm long, 4–7 μm diameter. *Spermatangia* terminal on primary and secondary fascicles and on involucre bracts, spherical to obovoid, 4–6 μm long, *c.* 4 μm diameter. *Gonimoblast* 1–2 per whorl, hemispherical, protruding wart-like from primary fascicle whorl, 100–140 μm broad, 50–70 μm high; carposporangia obovoid, 7–11 μm long, 6–7 μm diameter.

'Chantransia' stage not seen. (Figs 2c–e, 3).

DISTINGUISHING FEATURES:

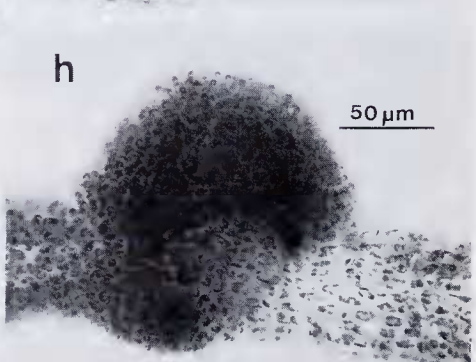
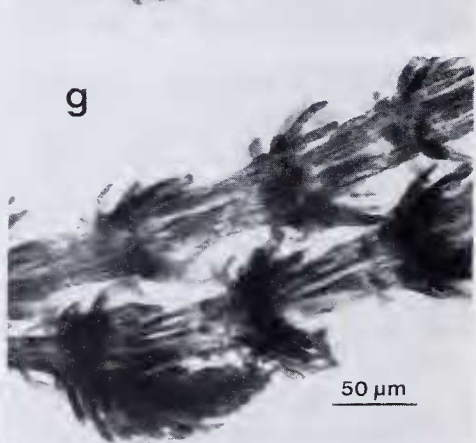
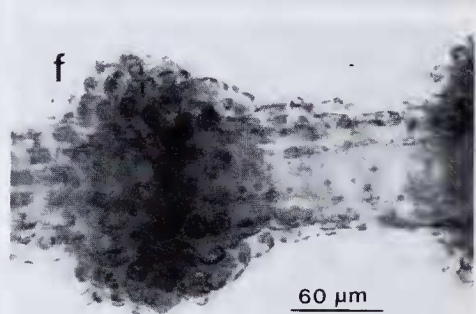
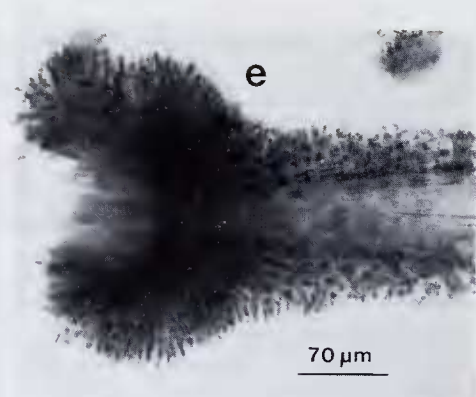
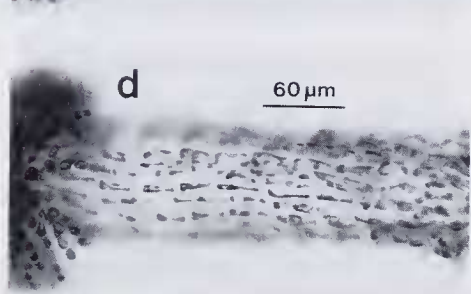
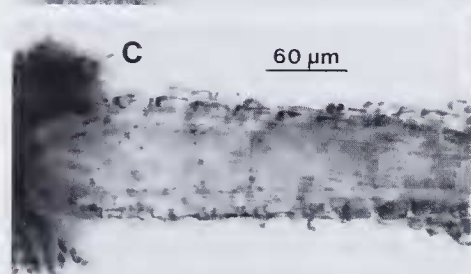
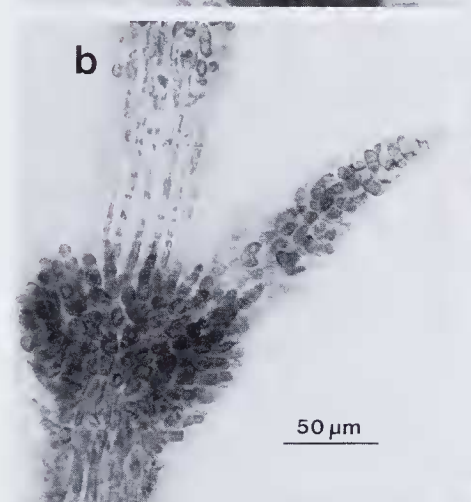
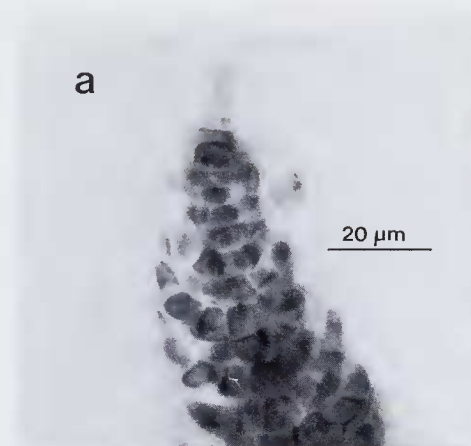
Batrachospermum atrum has tapering, acute branch apices with a protruding apical cell; whorls well-separated in young thalli (except sometimes near thallus apices); trichogynes club to urn-shaped; and gonimoblasts that protrude, usually wart-like, from the thallus. See also under distinguishing features of *B. diatyches* and *B. puiggarianum*.

DISTRIBUTION & HABITAT:

Africa, Asia, Australia, Europe, New Zealand, South America (Necchi 1990 & this study). Attached to rocks or plants (including other algae) in streams, less commonly in pools. Mature plants found in all months.

SPECIMENS EXAMINED:

The collections are divided into 3 groups based on the criteria discussed in the succeeding Taxonomic Notes. In addition to the specimens cited below, collec-



tions from Europe and New Zealand housed in BM were examined macroscopically and were all referable to *B. atrum* as delineated here.

Group (A).

Most cells in young fascicles cylindrical (L/D 1.2–3.3); mature fascicles little branched (usually > 1/2 number of cell storeys; 3–5 cell storeys, 0–2 times branching); whorls relatively open.

Australia: *Victoria* — Harris Creek, Buchan-Bruthen Road, 18.x.1984, *T.J. Entwisle* 701 (MEL); Darebin Creek, Ivanhoe, 26.x.1979, *G.T. Kraft s.n.* (MEL). *New South Wales* — Gordon, -.x.1915, *A.H.S. Lucas s.n.* (NSW), 20.xi.1915, *A.H.S. Lucas s.n.* (NSW). *Queensland* — Moggill Creek, -.x.1962, *J. Pebudy s.n.* (BR); Mt Coot-tha, Brisbane, 21.iv.1983, *A.B. Cribb* 963.2 (BR); Burnett Creek, 21.iv.1983, *A.B. Cribb* 742.7 (BR); Violet Gorge, Carnarvon Gorge, 14.viii.1990, *A.B. Cribb* 687.53 (BR).

New Zealand: *North Island* — Tikitiki Creek, Russell, 26.x.1938, *V.W. Lindauer* 135 (AD, NSW).

Asia: *Japan* — Musashi, 27.iv.1930, *M. Higashi s.n.* (UPS).

Europe: *Denmark* — Sjøland, 1.vii.1945, *T. Christensen s.n.* (UPS). *France* — Vire & Caen, Brittany, -.iii/vi.-, *Chauvin s.n.* (MEL), *s.d.*, *Chauvin s.n.* (MEL); Vire, Brittany, *s.d.*, *Lenormand* 326 (MEL), *s.d.*, *Anon* [ex Herb. Lenormand] (MEL, UPS); environs de Paris, 2.vi.1949, *E. Bornet s.n.* (UPS). *Germany* — Husbye, *s.d.*, *L. Hansen s.n.* (MEL), *s.d.*, *Suhr s.n.* (MEL); Erfurt, 25.ix.1835, *E. Caennere s.n.* (MEL). *Sweden* — Höör, 19.iv.1896, *H.G. Simmons s.n.* (UPS); 26.iv.1896, *O.R. Holmberg s.n.* (UPS); 29.vii.1909, *H. Kylin s.n.* (UPS); Väddö, 1.x.1934, *G. Israelson s.n.* (UPS); Bäve, Eriksfors, 21.vi.1990, *H. Kylin s.n.* (UPS); Bosjökloster, 30.vii.1909, *H. Kylin s.n.* (UPS).

Group (B).

Most cells in young fascicles rounded or barrel-shaped (L/D 0.8–2.0); mature fascicles richly branched (> 1/2 number of cell storeys; 3–6 cell storeys, 2–5 times branching); whorls compact.

Australia: *Victoria* — Tidal River, Wilsons Promontory, 8.iv.1981, *T.J. Entwisle* 39 (MEL), 24.vi.1983, *T.J. Entwisle* 271 (MEL), 16.iv.1990, *T.J. Entwisle* 1658 (MEL); McKenzies River, Zumsteins, 3.v.1981, *G.T. Kraft & T.J. Entwisle* 48 (MEL), 3.v.1981, *G.T. Kraft & T.J. Entwisle* 49 (MEL); Troopers Creek, Grampians, 18.v.1981, *P. Gabrielson & M. Barson s.n.* (MEL); Moor Moora Creek, Grampians, 18.ix.1990, *Entwisle* 1668 (MEL); Masons Falls, Running Creek, Kinglake National Park, 7.x.1987, *T.J. Entwisle* 1410 (MEL), 28.x.1987, *T.J. Entwisle* 1428 (MEL); Pheasant Creek, Flowerdale-Kinglake West Road, 24.i.1983, *T.J. Entwisle* 503 (MEL); W Tree Creek, Wulgulmerang-Buchen Road, *J.H. Ross & T.J. Entwisle* 1813 (MEL). *New South Wales* — Lyrebird Creek, Barren Grounds Nature Reserve, via Robertson, -.viii.1984, *A. Hardham & B. Gunning s.n.* (MEL), 11.xi.1988, *R.A. Andersen & T.J. Entwisle* 1566 (MEL); Dargans Creek, Clarence, Blue Mountains, iv.1918, *A.H.S. Lucas s.n.* (HO, NSW, UPS), 7.ii.1991, *T.J. Entwisle & P.M. McCarthy* (MEL). *South Australia* — Delamere, 21.iii.1987, *B.J. Brock s.n.* (AD, MEL); Wilpena Pound, Flinders Ranges, 24.xii.1965, *V. May s.n.* (NSW). *Queensland* — Pullenvale Creek, 12.x.1967, *J. Pebudy* (BRI). *Tasmania* — creek into Lake Fortuna, Western Arthurs, 8.xi.1982, *P.R. Robins & T.J. Entwisle* 103 (MEL); Cradle Mountain, *s.d.*, *L. Rodway s.n.* (HO); Launceston, xii.1844, *R.C. Gunn* 1826 (HO, NSW); Pool, Mt Field Plateau, xii.1910, *L. Rodway s.n.* (HO, NSW); creek into Lake Dove, 13.xii.1973, *A.B. Cribb* 773.3 p.p. (BRI).

New Zealand: *South Island* — tributary of Arthur River, Milford Sound, -.i.1971, *V. Stout* (S1) (MEL); tributary of Cleddau River, Milford Sound, -.i.1971, *V. Stout* (S3) (MEL); Island Stream, Oamaru, -.iv.1969, *M. Taylor* (T1) (MEL).

Europe: *England* — Yarmouth, *s.d.*, *Turner s.n.* (MEL). *France* — Deux-Ponts, 17.vii.1844, *Gümbel* 595 (MEL). *Germany* — Ausacker Mill, 30.iii.1832, *L. Hansen s.n.* (MEL); Würzburg, *s.d.*, *Anon.* (MEL); Husbye, *s.d.*, *Suhr s.n.* (MEL). *Sweden* — Tyringe, 2.viii.1909, *H. Kylin s.n.* (UPS).

Group (C).

Intermediate between group (A) and group (B).

Australia: *Victoria* — Swifts Creek, Eastern Victoria, 17.x.1984, *T.J. Entwisle* 695 (MEL); Swifts Creek, Swifts Creek Township, 28.x.1990, *J.H. Ross & T.J. Entwisle* 1797 (MEL); Murrindal River, Wulgulmerang-Buchan Road, 29.x.1990, *J.H. Ross & T.J. Entwisle* 1814 (MEL); Splitters Creek, near Wulgulmerang, 29.x.1990, *J.H. Ross & T.J. Entwisle* 1810 (MEL); young fascicles cells short cylindrical (L/D 1.6–2.0), mature whorls very open with short, little branched fascicles (cell storeys 3–4, branches 1–2), and apices crowded. *Queensland* — Lower dry Creek, Kroombit Tops, 11.xii.1983, *A.B. Cribb* 985.1 (BRI); as with Victorian specimens.

Europe: *France* — Vire, Brittany, *s.d.*, *Lenormand* 327 (MEL); young fascicle cells short cylindrical to globular (L/D 1.0–1.8), mature whorl structure difficult to decipher (cell storeys c. 5, branches c. 2); Bordeaux & Brittany, *s.d.*, *Bory de St-Vincent* 111 (MEL); young fascicle cells short cylindrical (L/D 1.2–2.0), mature whorl structure difficult to decipher (cell storeys c. 4, branches c. 1–3).

Fig. 3. *Batrachospermum atrum*. a — apex of thallus with protruding apical cell and immediate derivatives (*Entwisle* 1410). b — whorl of fascicles and young indeterminate lateral (*Entwisle* 76). c, d — internode of thallus at two different foci showing axial cell (c) and rhizoidal filaments (d) (*Hardham & Gunning s.n.*). e — relatively open whorl (*Hardham & Gunning s.n.*). f — relatively compact whorl (*Entwisle* 1566). g — open, loose whorl with long, cylindrical fascicle cells (*Lindauer* 135). h — compact whorl and protruding gonimoblast (*Entwisle* 1566).

TAXONOMIC NOTES:

The apices of all plants of *B. atrum* examined in the current study exhibited the following developmental pattern: the first laterals were cut off about 3–4 cells back from the apex and became 2-celled within the next 4 axial cells. The laterals initially consisted of cylindrical or globular cells with a dome-shaped to ovoid distal cell. In older fascicles, the cells were more rounded, eventually becoming barrel-shaped to globose. Hairs were often present, ranging in length from shorter than the apical cell to over 120 μm long. These observations concur with those of Necchi (1990) for *B. atrum*.

There was, however, considerable variation in the gross morphology of these plants. Some plants were quite distinctive in having one or more of the following features:

- i) profuse thallus branching,
- ii) thallus apices crowded by young fascicles,
- iii) globular, more compact shaped whorls, and
- iv) blunt — but still acute — rather than tapering thallus apices (apparently due to the shorter internodes).

There was no clear disjunction between any of these variants and plants with the more typical morphologies due to the presence of intermediate populations or even seasonal variation within populations.

The development and morphology of determinant laterals allowed two broad groupings to be recognized:

- i) with intercalary cells in young whorls cylindrical, and fascicles always little branched (group A), and
- ii) with intercalary cells in young whorls barrel-shaped or globular, and fascicles more or less richly branched (group B).

The first group typically had relatively long, brush-like whorls while the latter had more compact whorls. Once again, however, these differences could not be adequately quantified (or described) and a number of intermediate populations exist (Fig. 4). The distributional ranges of the two groups overlap considerably and there does not appear to be any obvious correlation between habitat and morphology (although water quality and stream velocity or turbulence could conceivably effect fascicle development; see also notes under *B. nothogae* at end of paper). Overmature specimens from a population usually referable to group (B) can resemble group (A) specimens due to the denudation of outer fascicle cells (exposing the more swollen inner cells). Because of the lack of a clear disjunction, these two groups are not given any taxonomic recognition. However, to facilitate any re-examination of this variation within *B. atrum* (and to promote the search for ecological and geographical variation), the specimens examined have been separated into three groups (including intermediate morphologies) based on the above criteria. New, probably non-morphological features, will be necessary to make any meaningful cleavage through the *B. atrum* assemblage.

HISTORICAL REMARKS:

In Georgian England, spring was heralded by the appearance of 'Slippery Pearl'd Black Hair' [or 'Black Beaded Conferva'] in select brooks and limpid rivulets (Dillenius 1741, Hudson 1778, Smith & Sowerby 1800, Dillwyn 1802). Although initially pale-green and delicate, by winter it darkened in colour and became quite bushy (Dillwyn 1802); late season plants were almost black, prompting Hudson (1778) to name it *Conferva atra*. Magnification of the thallus revealed minute mealy fibres at regular intervals, giving it a jointed appearance (Dillwyn 1802), and it was obviously related to *Conferva gelatinosa*, the 'Frog-spawn Conferva' (Smith & Sowerby 1800), but the whorls of laterals were distinctly smaller.

In 1797, Roth described the genus *Batrachospermum* to include a handful of algal collections, one of them carrying the Linnaean name *Conferva gelatinosa* (Linnaeus 1753). *Batrachospermum gelatinosum* (Linnaeus) de Candolle was not

formally described until 5 years later (de Candolle 1802), but is an earlier synonym for the widely used *B. moniliforme* Roth (1800).

In the early nineteenth century, many taxa were described in *Batrachospermum* by Carl Agardh, Bory St-Vincent, Kützing and Montagne, but the epithet '*atra*' remained largely ignored until Harvey (1841) transferred *Conferva atra* to *Batrachospermum*. Prior to 1841, a swag of names appeared in the literature for the 'Slippery Pearl'd Black Hair'. The nomenclature generally followed nationalistic (or linguistic) lines, with the English, the French and the Germans each devising their own names for this distinctive taxon.

On the continent, Bory de St-Vincent (1808) described 3 species of *Lemanea* from France which were later (Bory de St-Vincent 1823) transferred to the subgenus *Lemanines* of *Batrachospermum* (a subgenus equivalent to Sirodot's section *Sétacés* in circumscription). Sirodot (1884) reduced the three species to one,

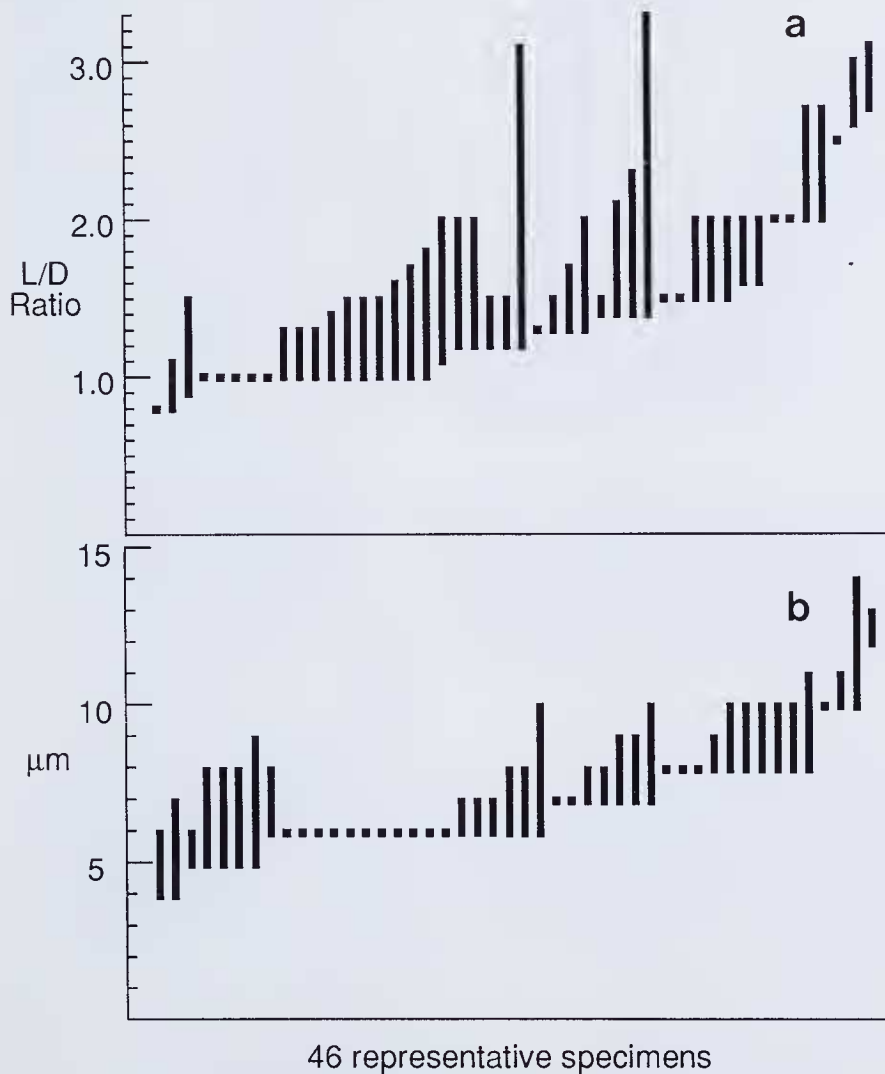


Fig. 4. Fascicle cell measurements of *Batrachospermum atrum*. a — intercalary cell length-to-diameter ratio in young fascicles. b — intercalary cell length in young fascicles (μm). Representative specimens taken at random from those examined.

Batrachospermum dillenii (Bory de St-Vincent) Bory de St-Vincent (with *B. atrum* as a synonym) but maintained a variety '*a. tenuissimum*' for slender plants with poorly developed whorls and fewer secondary fascicles. A second species was added to the section *Sétacés*, *B. gallaei* Sirodot, which had spermatangia and carpogonia borne on separate plants and occasional gonimoblasts arising from rhizoidal filaments.

In the German literature, a range of varietal names exist for taxa equivalent to *B. atrum*: Carol Agardh (1817) used '*Batrachospermum moniliforme* β *detersum*' for setaceous species of *Batrachospermum*, whereas Kützing (1849) used Agardh's epithet as well as '*B. vagum* β *tenuissimum*' (based on *Conferva atra* sensu Smith & Sowerby 1800 = *C. atra* Hudson) and '*B. vagum* γ *detersum*' (based at least partly on *Lemanea sertularina* = *B. dillenii* Sirodot). Rabenhorst (1868) introduced the names '*B. moniliforme* i. *atrum*' (based on *B. atrum*) and '*B. vagum* e. *dillenii*' (based on *B. dillenii*) for two apparently different plants. Other synonyms exist in the genus *Torularia* Bonnemaison (= *Batrachospermum*) as well as *Batrachospermum* (e.g. see De Toni 1897, p. 57).

The English, following Harvey (1841), used *B. atrum* (e.g. Cooke 1882–4, Hassall 1845), in the case of Cooke (1882–4) with the addition of a curious varietal name — '*B. atrum* var. *dillenii*'. Following Sirodot (1884), however, the names *B. dillenii* and *B. gallaei* (the former monoecious, the latter dioecious) were used widely throughout the world (e.g. Pascher & Schiller 1925) until Israelson (1942) resurrected *B. atrum* and proposed the synonymy of both Sirodot's setaceous species. Recently, Necchi (1990) has also referred the African alga described as *B. angolense* W. West & G.S. West (1897) to *B. atrum*.

A number of taxa apparently distinct from *B. atrum* have been recognized among the setaceous *Batrachospermum* species, and Necchi (1990) discusses the affinities of most of these. *Batrachospermum puiggarianum* is the only other setaceous taxon retained by Necchi (1990), although *B. orthostichum*, originally included in the section *Setacea*, is transferred by Necchi to the section *Turficola* due to the presence of indeterminate as well as determinate gonimoblast filaments.

3. *Batrachospermum puiggarianum* Grunow in Wittrock & Nordstedt, *Algae Exsic.* 11: 1, no. 501 (1883). *Batrachospermum atrum* var. *puiggarianum* (Grunow) Necchi, *Bolm Bot.* 11: 25 (1989).

HETEROTYPIC SYNONYMS: *Batrachospermum schwackeanum* Möbius, *Ber. dt. bot. Ges.* 10: 20, pl. 1 figs 1–8. (1892).

Batrachospermum nigrescens W. West & G.S. West, *J. Bot.* 35: 2 (1897). *Sirodotia nigrescens* (W. West & G.S. West) Skuja, *Bol. Soc. bot.* 34: 54 (1960).]

TYPUS: Apiaí, São Paulo, Brazil. Coll. Y.I. Piggari s.n., some time prior to 1883 (S). [Type material not examined]

Tufty, stream-inhabiting alga. *Thallus* rigid, up to 6 cm long and 80–300 μ m diameter; branching irregular, frequent, acute to perpendicular. *Whorls* inconspicuous, obconical or pear-shaped, separated or contiguous, compact; internodes 200–1000 μ m long. *Thallus apices* long tapering, acute; apical cell dome-shaped, c. 6 μ m long, c. 7 μ m diameter, L/D c. 1; subsequent axial cells globular, and finally cylindrical; first laterals cut c. 3 axial cells back from apex, becoming 2-celled c. 10 or more axial cells from apex; young fascicles indiscernible, appearing as packets of globular cells tightly corticating each node. *Young central axis* [100–500 μ m from apical cell] consisting of axial cells c. 8–25 μ m diameter, clothed by rhizoidal filaments c. 6 μ m diameter and resembling the fascicles, axial cell c. 3–4 times broader than rhizoidal filaments. *Mature central axis* consisting of broad axial cells, c. 40–80 μ m diameter, clothed by rows of rhizoidal filaments, c. 4 μ m diameter. *Fascicles* 2 per pericentral cell (plus rhizoidal filament), branching 1–2(–3) times, with 2–5 cell storeys; cells 7–18 μ m long, 6–12 μ m diameter, proximal

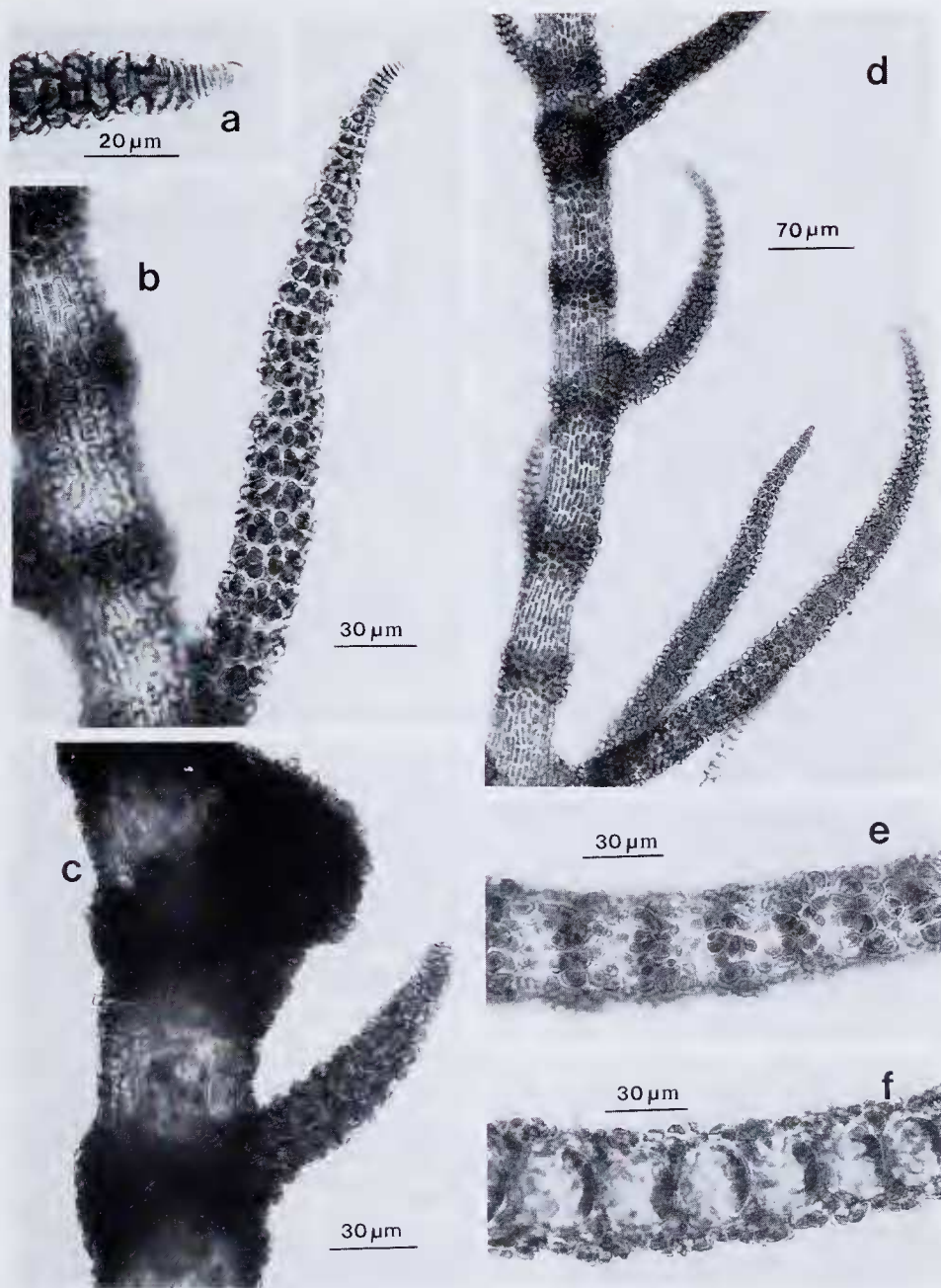


Fig. 5. *Batrachospermum puiggarianum* (Paula s.n.). a — apex of thallus with protruding apical cell and immediate derivatives. b — whorl structure in young indeterminate lateral and mature axis. c — gonimoblast protruding from top whorl and indeterminate lateral arising from bottom whorl. d — thallus habit showing appearance. e, f — internode of thallus at two different foci showing rhizoidal filaments (e) and young rhizoidal filaments and compact fascicles (f).

and intercalary cells finally barrel-shaped or cylindrical, apical cell conical; hairs absent to abundant, long. *Secondary fascicles* frequent, similar to primary fascicles near axial cell nodes but only unicellular to few-celled away from nodes in younger thalli, eventually extending from one node to next.

Monoecious or dioecious. *Carpogonial branches* relatively common in primary fascicles, borne on pericentral cell or proximal cell of fascicle, protruding from whorl, 1–3 cells long, straight or curved, with compact, few-celled involucre bracts not reaching trichogyne. *Carpogonia* 8–32 μm long; trichogyne club-shaped or elliptic, 5–9 μm diameter. *Spermatangia* terminal, rarely subterminal, on primary and secondary fascicles, spherical to obovoid, 4–7 μm diameter. *Gonimoblast* 1–2(-3) per whorl, hemispherical, protruding wart-like from primary fascicle whorl, 90–220 μm broad, 50–130 μm high; carposporangia obovoid to elliptic, 8–13 μm long, 6–11 μm diameter. [Description adapted from Necchi 1990, pp. 172–173, with additional information from specimen examined] (Figs 5, 6)

DIAGNOSTIC FEATURES:

B. puiggarianum differs from *B. atrum* in having thallus apices with very compact whorls which appear as clusters of cells tightly corticating the node rather than as branched fascicles. Subsequent division of the primary fascicle initials seems to occur at least 10 axial cells from the apex of the thallus.

DISTRIBUTION & HABITAT:

Angola (Africa), and Argentine, Brazil and Uruguay (South America). Attached to rocks or plants in moderate to fast flowing streams (Necchi 1990). Mature plants found throughout the year (Necchi 1990).

SPECIMEN EXAMINED:

Brazil — Monte Mor, Capivari Mirim River, 27.vii.1975, E.J. Paula (SP, MEL).

TAXONOMIC NOTES:

Batrachospermum puiggarianum has been distinguished from *B. atrum* primarily on the basis of its very compact whorls, in which individual fascicles cannot be discerned. In addition to whorl compactness, the illustrations of *B. puiggarianum* by Necchi (1990) show an apex with globular lateral initials, no 2-celled laterals until some 13 cells proximal to the apex, and an indiscernible fascicle structure. Although Starmach (1977) used the absence of secondary laterals to characterize *B. puiggarianum*, Necchi (1990) found secondary laterals to be abundant in the material he observed (including the holotype).

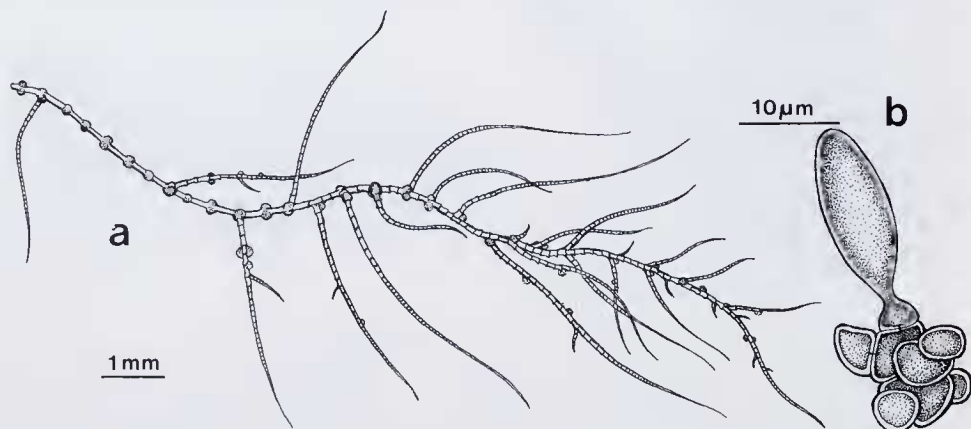


Fig. 6. *Batrachospermum puiggarianum* (Paula s.n.). a — habit. b — carpogonial branch.

Observations on Brazilian material of *B. puiggarianum* made during the current study have confirmed the findings of Necchi (1990) that this taxon is indeed distinct from *B. atrum*. The young thallus apices are quite different: with their tightly corticating fascicles (the structure of which is hardly discernible), they resemble superficially species of Lemnaceae or even *Ceramium* (Rhodophyta, Ceramiales) more than *Batrachospermum*. In the young whorls, the fascicle cells are mostly globular and seldom longer than wide. Although some specimens of *B. atrum* with compact whorls may resemble this species, an examination of young, healthy thallus apices should be sufficient to correctly separate them.

SYNONYMY & ALLIED TAXA

In an unpublished list of *Batrachospermum* species (held at UPS), Skuja lists the following published and unpublished species in the section *Setacea* (with his comments in square brackets): *B. dillenii* [dioecious], *B. nothogaeae*, *B. gallaei* [monoecious], *B. gallaei* var. *longipilum* [New Zealand], *B. protimum* nom. ms. [Liberia; monoecious], *B. annulatum* nom. ms. [U.S.A.; monoecious], *B. africanum* Rabenhorst [? *Sirodotia*; dioecious; Africa], *B. puiggarianum* [Brazil], *B. schwackeanum* [monoecious], *B. orthostichum* [Brazil; monoecious], *B. patens* Suhr [S. Africa; monoecious] and *B. sirodotioides* n. sp. [monoecious].

I have not seen any material of, or published reference to, '*B. protimum*', '*B. annulatum*' and '*B. sirodotioides*', and their status must await further study. The proposed synonymy by Necchi (1990) of *B. schwackeanum* (and *B. nigrescens*) with *B. puiggarianum*, and *B. angolense* with *B. atrum*, was based on an examination of type materials and his familiarity with the *Batrachospermaceae* flora of Brazil, and his judgements are accepted here. Israelson (1942) argued convincingly for the synonymy of *B. gallaei* and *B. dillenii* with *B. atrum* (see also Historical Remarks under *B. atrum*). The other taxa are considered below.

B. africanum Rabenhorst, *Allg. Deutsche Naturhist. Zeitung* n.s. 1: 281 (1855).

An isotype of this species at MEL includes a mixture of two *Batrachospermum* species, one probably referable to section *Sirodotia* (although no reproductive structures were observed) and the second to *B. puiggarianum* or *B. atrum*. Although the mature whorls of the latter plants were similar to those of *B. puiggarianum*, the young thallus apices seemed to be more like those of *B. atrum*. Due to the lack of good apical material, a definitive determination of the latter plants cannot be made. In any case, since Rabenhorst (1855) interpreted the two taxa on this sheet as growth forms of a single species, the application of the name *B. africanum* is unclear. Consequently, *B. africanum* Rabenhorst remains as a species *inc. sed.*

B. gallaei var. *longipilum* Skuja nom. nud.

Skuja described this variety (Skuja-Tyler corr., 19.ii.1970) as having rather undeveloped laterals and conspicuous, numerous, long hairs. This manuscript name originally was coined for 2 collections from New Zealand: Avon River, Christchurch (*Laing* 1101) and Te Henga (*L. Cranwell*, 7.vii.1931). From Skuja's illustrations of these species (Figs 7, 8), they are clearly referable to *B. atrum* as circumscribed here.

Hair formation in algae is often environmentally controlled: e.g. by light regime (Dixon 1973; for Floridiophycidae) or nutrient status of the water (e.g. *Stigeoclonium* produces profuse, long hairs in nitrogen and phosphorus deficient media and no hairs in nutrient enriched media; pers. obs.). Hair abundance and length were extremely variable in the material of *B. atrum* examined and are unlikely to indicate more than an ecomorph [corroborating the findings of Necchi (1988) for various *Batrachospermum* species from Brazil].

Five additional New Zealand collections were later referred to this variety: Cowans (*L.M. Cranwell*, 17.ix.1932); Anawhata (*L.M. Cranwell* 1932/1, 17.vii.1932); Maheno (*M. Taylor*, 16.iii.1969); Tucker Point, Auckland

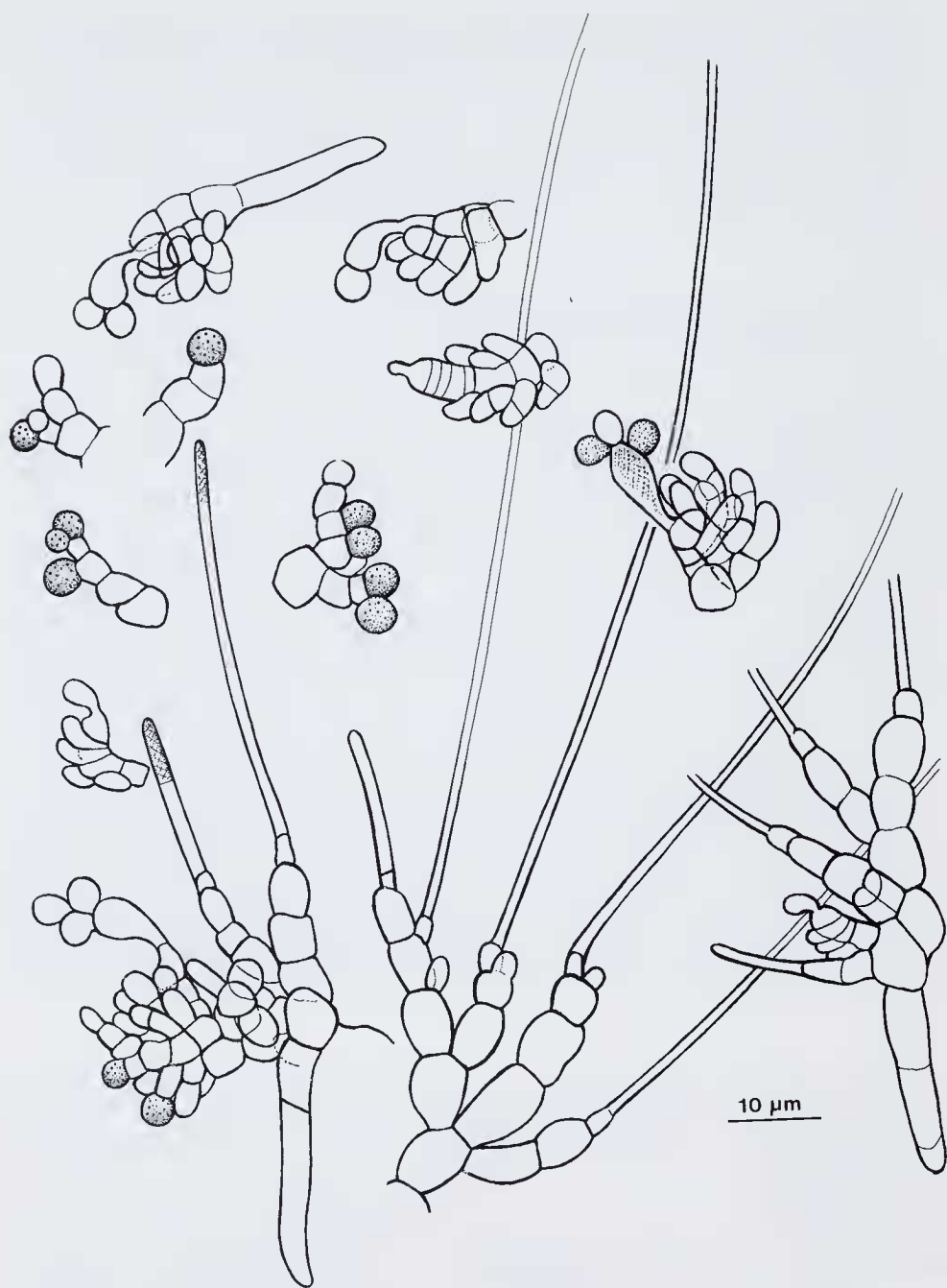


Fig. 7. *Batrachospermum gallaei* var. *longipilum* Skuja *nom. nud.*. Unpublished sketches by H. Skuja (redrawn by Anita Barley) from material collected at Te Henga, New Zealand (*Cranwell s.n.*). They show spermatangium, carpogonial branches and fascicles terminated by long hairs. This material is referable to *B. atrum* as circumscribed in this paper.

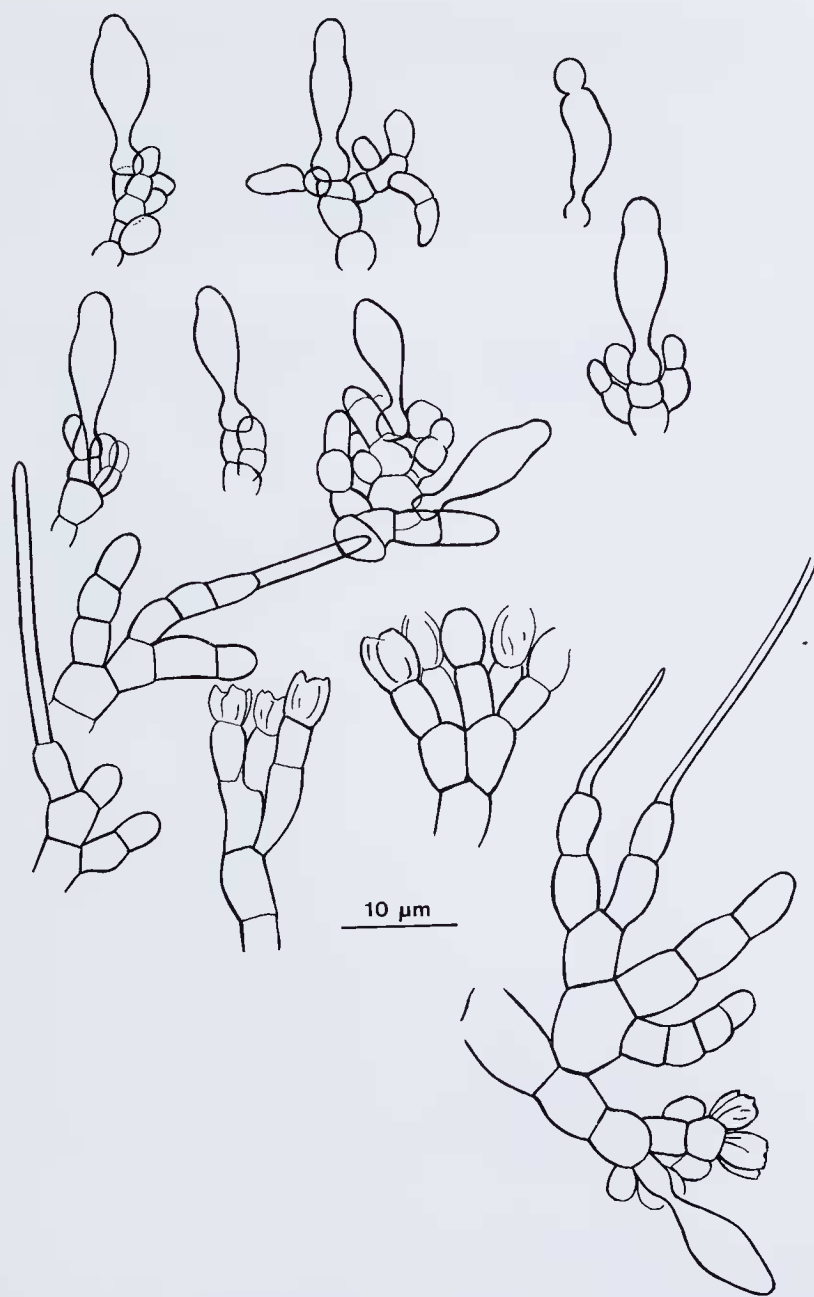


Fig. 8. *Batrachospermum gallaei* var. *longipilum* Skuja *nom. nud.* Unpublished sketches by H. Skuja (redrawn by Anita Barley) from material collected from the Avon River, Christchurch, New Zealand (Laing 1101). They show carpogonial branches, empty spermatangium and hairs terminating fascicle cells. This material is referable to *B. atrum* as circumscribed in this paper.

Island (K. Wise, 19.i.1963: 'probably var. *longipilum*'); and Torbay Falls, Auckland (M. Seager, 24.x.1953). [A further collection from Tikitikiora Creek, Bay of Islands (V.W. Lindauer 135, 26.x.1938) in AD and NSW is labelled as *B. gallaei* var. *longipilum* but does not have any hairs and was not determined by Skuja.]

Skuja also identified three Tasmanian collections as *B. gallaei* var. *longipilum*: bog pool, Mt Wellington (Tyler 660609/4); North Lake, Mt Picton (Tyler 690201/1); and Creek No. 2, into Lake Pedder (Tyler 691126/1). Photomicrographs of a later collection from the bog pool on Mt Wellington show a setaceous plant with compact whorls of discernible structure, rounded fascicle cells and abundant, very long hairs.

Skuja described *B. dillenii* as a dioecious alga with more strongly developed laterals and shorter fewer hairs than '*B. gallaei* var. *longipilum*'. This probably allies *B. dillenii* with *B. atrum* group (A) as defined above. [His interpretation of the Queensland material referred to *B. dillenii*, based on an examination of published illustrations (Möbius 1895, pl. 1 figs 1–7; reproduced in Bailey 1895), is that it is probably misidentified].

B. nothogae Skuja nom. nud.

This manuscript name was devised by Skuja for two collections from the Falkland Islands and New South Wales, Australia (see Historical Remarks under *B. diatyches*). A third population, from Lake Pedder (here described as *B. diatyches*) in Tasmania, Australia, was viewed as a possible variety of this species [Tyler-Skuja corr., 23.iv.1968: annotation on letter by Skuja reads: '660303/2 — *Batrachosp. nothogae* Skuja in Mspt. var.'].]

The Falkland Islands collection [William Stanleys Haven, 1850s, *Lechler s.n.* (UPS)] has very compact, reduced whorls whose structure can be barely discerned, and the fascicles are certainly not like those of *B. diatyches*. There are few young apices in the herbarium material examined, but one observed was tapering with a protruding apical cell. This population may be referable to either *B. atrum* or *B. puiggarianum*.

The New South Wales alga, from Clarence in the Blue Mountains (-iv.1918, A.H.S. Lucas s.n.; 7.ii.1991, T.J. Entwistle & P.M. McCarthy), has relatively diminutive whorls, but still falls within the broadly circumscribed *B. atrum* accepted here. Variants similar to those from Clarence also occur in other acidic, electrolyte poor, sandstone areas near Sydney and Woollongong. Elsewhere in Australia and overseas, *Batrachospermum atrum* is mostly found in alkaline, hard-water (but relatively pristine) streams. The sandstone populations of *B. atrum* appear to have distinctive ecological requirements, which may support their recognition as a distinct taxon should good diagnostic characters be found at some later date.

The Lake Pedder material is clearly distinct from the other two collections, but due to Skuja's obvious intention that the New South Wales and Falkland Islands algae represent what he perceived as '*B. nothogae*', that name is unsuitable for the new taxon described in this paper. '*B. nothogae*', therefore, will remain a *nomen nudum* unless later revisionists wish to revive Skuja's taxon (and use his epithet).

B. orthostichum Skuja, *Hedwigia* 71: 84, pl. 2 figs 1–15 (1931).

Two species in the section *Turficola*, *B. orthostichum* and *B. keratophytum* (*sensu* Necchi 1990), can have reduced whorls but are quite different from *B. atrum*. *Batrachospermum orthostichum*, although producing *atrum*-like fascicles, has relatively well-developed, confluent whorls. It also has club-shaped thallus apices and both determinate and indeterminate gonimoblast filaments (Necchi 1990 and pers. obs. on Brazilian material from SP).

B. patens Suhr, *Flora* 23: 296–297 (1840).

This species was based on a collection from Cape Kroemsrivier, South Africa (1839, Drège), part of which is housed at MEL. The thallus apices are rounded, the

fascicles curved, and with most cells short-cylindrical to barrel-shaped and proximal cells long-cylindrical. The globular gonimoblast protrudes from the whorl, but is like a denser and broader vegetative whorl rather than a 'wart-like' protuberance. Some gonimoblast filaments extend along the internode and are presumably indeterminate. The MEL plants closely resemble *B. keratophytum* as delineated by Necchi (1990), a taxon conceived somewhat differently by Entwisle (1984, 1989). The North American interpretation of this taxon appears to be different again (based on herbarium material held in MEL), so that the circumscription of *B. keratophytum* and related taxa, such as *B. patens*, needs to be critically assessed based on the re-examination of available types. That analysis is beyond the scope of this study.

B. tenuissimum Bory de St-Vincent, *Dict. class. hist. nat.* 227 (1823). *B. dillenii* var. *tenuissimum* (Bory de St-Vincent) Sirodot, *Batrachospermes* 256, pl. 20 figs 3,4, pl. 21 figs 13–16 (1884). *Lemanea batrachospermosa* Bory de St-Vincent, *Annls. Mus. natl. Hist. nat.* 12: 188, pl. 25, figs 3,4 (1808).

Most French collections referred to this species belong to *B. atrum* group (A), and this informal grouping may be the taxon Bory de St-Vincent perceived as distinct from *B. dillenii* [although some French collections referable to *B. atrum* group (A) from the same region have been identified as *B. dillenii sensu str.*]. Sirodot (1884, p. 256) found both slender growth forms ('var. *tenuissimum*') and broad growth forms ('typical variety') in a mountain spring. He surmised that the slender thalli were produced in shaded habitats with low water levels. Although Sirodot accepted Bory de St-Vincent's taxon at the varietal level, he appeared to be convinced that it was no more than a growth form of *B. dillenii*.

MONOPHYLY

Whether or not the species defined here are monophyletic, cannot be determined at this stage. The major developmental differences between *B. diatyches* and the other two species — such as apical cell size and disposition, and the shape and development of determinate laterals — suggest that this may in fact not be the case. There is certainly no evidence to support the homology of reduced whorls in the three taxa.

The mature thalli of the setaceous *Batrachospermum* species have determinate laterals which are unilaterally branched, curved, and consisting of predominantly cylindrical or barrel-shaped cells throughout. These 'audouinelloid-like' fascicles (Necchi 1988) closely resemble the prostrate phase ('Chantransia') found in almost all *Batrachospermum* life histories. The mature thalli of most, but not all, other *Batrachospermum* species have freely branched laterals consisting of rounded, ovoid or bone-shaped cells. Since there are no 'Chantransia' phases with nonaudouinelloid-like cells and it could be argued that the audouinelloid-like morphology is the more general state in the genus. The problem with this argument lies in the homology of the characters: are audouinelloid-like laterals in the macroscopic phase homologous to the filaments of the 'Chantransia' phase? If they are homologous, the setaceous *Batrachospermum* are defined by a plesiomorphic character and are an unnatural (paraphyletic) group. If they are not homologous, we do not know whether the group is monophyletic or paraphyletic. It seems less likely that dissimilar cell morphologies between the life phases of an ancestral taxa would converge to produce what now appear to be a homologous states (but see Gabrielson & Garbary 1987, who conclude that the resolution of ancestral states from heteromorphic vs isomorphic generations is irresolvable). That all 'audouinelloid-like' cells in *Batrachospermum* are homologous and plesiomorphic seems, to me, to be a reasonable, and parsimonious, assumption. This would imply that the three setaceous *Batrachospermum* species do not form a monophyletic group since they share no apomorphies.

In any case, due to the phenetic similarities between *B. atrum*, *B. puiggarianum* and *B. diatyches*, a detailed comparison of the group has been necessary before any taxonomic entities could be clearly delimited. Later analyses may well show that the setaceous taxa considered in this paper do not share a common ancestor unique to themselves, even though as a morphological group the three taxa are best defined in reference to one another.

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